

## COMPARATIVE SUCCESSIONAL ROLES OF TREMBLING ASPEN AND LODGEPOLE PINE IN THE SOUTHERN ROCKY MOUNTAINS

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**ABSTRACT.**— A review of the ecological distribution and successional roles of lodgepole pine and trembling aspen in the Southern Rocky Mountains suggests that the two species have different strategies for occupying disturbed sites. Lodgepole pine's easily dispersed seeds and faster growth from seed in unsuppressed conditions allows it to colonize severe burns, even from remote seed sources. Aspen appears to compensate for ineffective development from seed by vegetative reproduction from durable root stocks, which promotes geographic persistence. Such persistence is achieved by the maintenance of a forest structure conducive to light surface fires, which stimulate suckering and retard conifer invasion, and by the accumulation of soil organic matter, which improves site nutrient retention and water availability.

Empirical studies of the dynamics of trembling aspen (*Populus tremuloides*) and lodgepole pine (*Pinus contorta* ssp. *latifolia*) forests show that both tree species commonly colonize open sites following disturbance (Clements 1910, Ives 1941, Stahelin 1943, Marr 1961, Langenheim 1962). In portions of the upper montane and subalpine zone (2,400–3,000 m) of the Southern Rocky Mountain region, the geographic and habitat ranges of these two important colonizers overlap, so that either species (or both) might be encountered on a disturbed site. Within this zone of cooccurrence, neither the site preferences of nor the successional relationship between these two species is satisfactorily detailed (Marr 1961, Peet 1981). Regarding habitat range, early workers thought that aspen more frequently occurred on mesic sites, and lodgepole more commonly occupied drier settings (Bates 1924, Daubenmire 1943). More recently, Marr (1961) and Peet (1978) have questioned the simplicity of this arrangement. Peet (1978) asserts that both species possess a comparable ecological optimum on mesic sites in the lower/middle subalpine zone, as evidenced by the distribution of aspen in mountainous regions where lodgepole is absent. He observed that, in regions where both species occur, lodgepole is a better competitor than aspen on prime sites and therefore tends to preempt aspen from optimal settings. Aspen maintains popu-

lations in this region of cooccurrence by possessing a broader environmental tolerance range, often being restricted to a variety of both wetter and drier sites at higher and lower elevations than lodgepole.

The successional relationship of the two species in this region of cooccurrence is complex (Moir 1969, Reed 1971, 1976, Whipple and Dix 1979, Peet 1981). Differences in their respective patterns of colonization are likely related to a number of factors, chief among which is the fundamental dissimilarity in their reproductive strategies. Lodgepole is a prolific seeder, depending on widespread wind dispersal of its light seeds to facilitate invasion of disturbed sites. Aspen, although it is capable of reproduction by seed, more often reproduces by vegetative suckering. Marr (1961) observed that aspen roots often survive fire, thus providing a stock for vegetative propagation on burned sites. Furthermore, both Marr (1961) and Peet (1981) noted that aspen is often found in the understory of a variety of different forest covers, including dense, mature conifer forests. Thus, aspen is able to maintain a suppressed but viable population on a site through long periods of time, and is capable of colonizing burned sites by the release of the persistent rock stock. Horton and Hopkins (1965), in an examination of fire ecology in aspen groves, found that light burns (i.e., low temperatures) stimulate aspen suckering (probably through

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both the reduction of competition with the thick ground layer and mobilization of the nutrient supply tied up in the ground layer vegetation), but heavy burns (i.e., high temperatures) inhibit aspen suckering (presumably through damage to perennating organs in the root stock). Heavy burns are likely to enhance the establishment of lodgepole pine on disturbed sites, because they create a mineral seedbed and eliminate much of the ground layer vegetation that might normally inhibit development from seed of lodgepole pine. Hence, postburn colonization of sites by either aspen or lodgepole in their zone of cooccurrence is influenced by their respective reproductive modes and ecological tolerances of environmental factors, by burn intensity, and by a chance element (Marr 1961) associated with the probability/proximity of a lodgepole seed source or an aspen rootstock.

The present study presents a review and interpretation of both the habitat ranges and successional relationship of lodgepole pine and trembling aspen in the Colorado Front Range. This discussion is accompanied by a data set examining the age/size structure and community characteristics of an abrupt aspen/lodgepole ecotone on the south flank of Bierstadt Moraine in Rocky Mountain National Park, Colorado.

Bierstadt Moraine is a lateral moraine of approximately 200 m relief, deposited by alpine glaciers during the late Wisconsin glacial maximum (Pinedale stage, Richmond 1960). Bierstadt Moraine trends slightly north of east, extending for approximately 6 km along the northern margin of the Glacier Basin Campground. The dominant particle size in the till is sand (exceeding 70 percent of the total fine earth fraction); soils developed under both aspen and lodgepole forests are immature (typic Cryorthents), although there are distinct differences in the A-horizon under each cover type. A transect down the south-facing slope of Bierstadt Moraine from top to bottom reveals the following sequence of plant communities: lodgepole pine forest on the gently rolling upland, sagebrush (*Artemisia* ssp.) scrub on the steep upper slope, aspen forest on the middle slope, and lodgepole

pine forest on the lower slope and throughout the adjacent valley bottom. The ecotone studied is between the aspen forest and the lower lodgepole forest, at an elevation of 2,700 m.

The study area is located within a much larger region (perhaps 10 km<sup>2</sup>) which was burned by the Bear Lake fire of 1900 (Peet 1981). None of the trees cored on the study site is older than this burn, so that the modern forest is representative of postburn recovery dating three-quarters of a century from this extensive fire.

#### METHODS

Seven 4 × 60 m belt transects were placed with their long-axis oriented normal to elevation contours and the aspen/lodgepole ecotone. Each transect was subdivided into six 4 × 10 m quadrats and placed so that three of these quadrats were under aspen cover and three were under lodgepole cover. Although precise location of the "boundary" between types is subjective, in this case abrupt differences in both litter type and ground cover were used to determine the midpoint of the belt transect. Belt transects were spaced along the flank of the moraine at intervals of 60 m. In each quadrat, all living trees (stem DBH > 6.25 cm) were identified to species and their diameter recorded. All saplings (0 < stem DBH < 6.25 cm) and seedlings (stems less than breast height) in each quadrat were counted by species. All standing dead stems in each quadrat were counted by species. Along the central long axis of each belt transect, the coverage of all herbs and shrubs was determined in 10-m intervals by the line-intercept method (Canfield 1941). In two of the seven belt transects a radial core was extracted from each tree (at 0.3 m height) with an increment borer, and the tree's age determined. Measurements of slope aspect, steepness, and configuration were taken for each 4 × 10 m quadrat. In two of the belt transects, the type and depth of litter was measured, using a point-frame, at the center of each 4 × 10 m quadrat. The point-frame was 1 m wide, with a 5 cm recording interval; hence, there are 21 litter measurements per quadrat. In addition, two soil pits were dug, one under each cover type, and the soil profiles were described.

TABLE 1. Vegetation data by forest type.

| Characteristic  | Lodgepole cover |       | Aspen cover |       |
|---|-----------------|-------|-------------|-------|
|   | Lodgepole       | Aspen | Lodgepole   | Aspen |
| Tree density<br>(stems·ha <sup>-1</sup> )               | 2420            | 430   | 100         | 2800  |
| Stand basal area<br>dm <sup>2</sup> ·ha <sup>-1</sup> ) | 2280            | 170   | 140         | 1910  |
| Mean diameter<br>(cm·stem <sup>-1</sup> )               | 15.5            | 10.2  | 19.5        | 13.2  |
| Sapling density<br>(st·ha <sup>-1</sup> )               | 290             | 190   | 80          | 540   |
| Seedling density<br>(st·ha <sup>-1</sup> )              | 10              | 210   | 20          | 3870  |
| Standing dead density<br>(st·ha <sup>-1</sup> )         | 250             | 920   | 10          | 2510  |

RESULTS

The aspen forest on the south flank of Bierstadt Moraine is on a slightly steeper slope than the lodgepole forest (15° vs. 12°), fingering to lower elevations along local convexities of the slope face.

The principal difference in the soil profiles under each cover type is the presence of a dark brown (10 YR 3/2) surface mineral horizon, approximately 10 cm thick, under the aspen forest. This darker topsoil, which is absent under lodgepole, is indicative of higher organic matter content associated with humification of the deciduous aspen leaves and litterfall from the thick ground layer vegetation (cf Hoff 1957, Tew 1968). Hydrometer analysis (Bouyoucos 1962) of soil material collected from varying depths in both profiles revealed no meaningful differences in texture

with depth or between profiles, all samples being coarse sandy loams. This texture, which normally would permit only low water retention and rapid leaching of cations, imparts increased significance to the organic buildup in the A-horizon under aspen (Morgan 1969), in that organic colloids increase the water retention capacity and the cation (or nutrient) exchange capacity of the aspen soil relative to the lodgepole soil.

The ground layer of the lodgepole forest was poorly developed, with 3 percent ground coverage divided evenly between herbs and woody shrubs. The aspen forest ground layer was well developed (58 percent ground cover) and almost exclusively herbaceous. Such differences between aspen and conifer ground layer development have been reported elsewhere (Hoff 1957, Marr 1961, Peet 1981) and apparently result from a combination of the high acidity of conifer litter (Daubenmire 1953) and increased light penetration to the forest floor under aspen (particularly in the spring prior to aspen leaf flush).

Under the lodgepole cover, tree density was 2,850 stems·ha<sup>-1</sup>; lodgepole pine accounted for 84.9 percent of this total (Table 1). Under the aspen cover, tree density was 2,900 stems·ha<sup>-1</sup>; aspen accounted for 96.6 percent of this total. Similarly, under lodgepole cover, stand basal area was 2,450 dm<sup>2</sup>·ha<sup>-1</sup> (93.1 percent lodgepole); under aspen cover, stand basal area was 2,050dm<sup>2</sup>·ha<sup>-1</sup> (93.2 percent aspen).

Little evidence of invasion by more tolerant tree species over the last 75 years exists. The only other tree species encountered were

TABLE 2. Cross transect patterns of mean tree basal area and understory representation by species.

| Cover/Quadrat/Species |             | Mean tree<br>Basal area<br>(dm <sup>2</sup> ·stem <sup>-1</sup> ) | Number of saplings<br>and seedlings | Number of<br>standing dead |
|-----------------------|-------------|---|-------------------------------------|----------------------------|
| Lodgepole<br>cover    | 1 Lodgepole | 1.74  | 10                                  | 9                          |
|                       | 1 Aspen     | 0.47  | 9                                   | 12                         |
|                       | 2 Lodgepole | 1.68  | 5                                   | 5                          |
|                       | 2 Aspen     | 0.37  | 10                                  | 9                          |
|                       | 3 Lodgepole | 2.34  | 10                                  | 7                          |
|                       | 3 Aspen     | 0.89  | 15                                  | 56                         |
| -----Ecotone-----     |             |   |                                     |                            |
| Aspen<br>cover        | 4 Lodgepole | 2.52  | 3                                   | 0                          |
|                       | 4 Aspen     | 1.21  | 121                                 | 92                         |
|                       | 5 Lodgepole | 1.47  | 2                                   | 0                          |
|                       | 5 Aspen     | 1.45  | 125                                 | 60                         |
|                       | 6 Lodgepole | 4.91  | 4                                   | 1                          |
|                       | 6 Aspen     | 1.47  | 124                                 | 59                         |

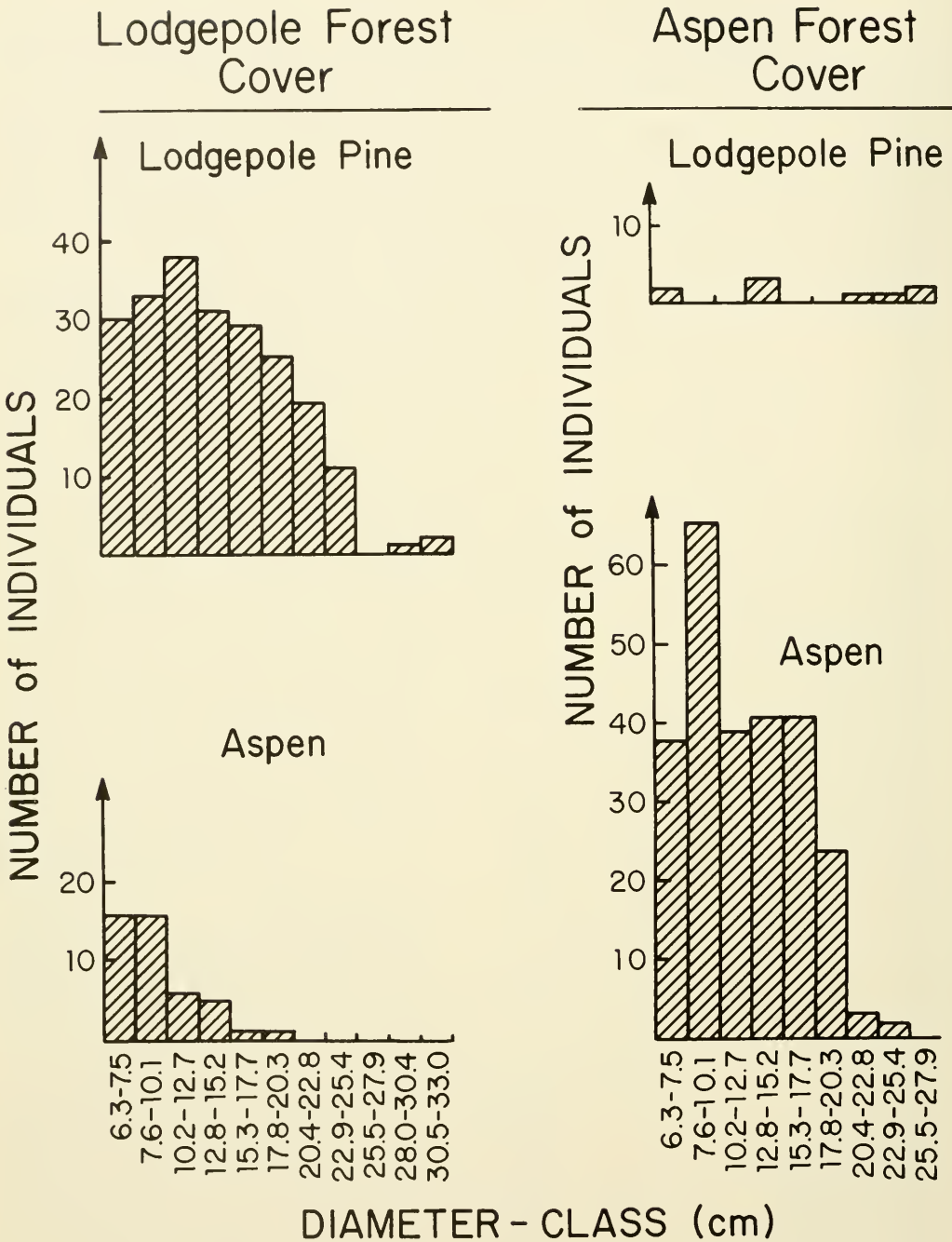


Fig. 1. Diameter-class distribution by forest cover. Histograms of stem number by diameter class for both lodgepole pine and aspen under each forest cover are depicted (diameter class interval = 2.54 cm). The number of stems in the smallest diameter class (6.3-7.5 cm) has been doubled to adjust for its half-interval width.

willow (*Salix* spp.), with two saplings present in a quadrat adjacent to the valley bottom, and Douglas-fir (*Pseudotsuga menziesii*), with a single seedling found under aspen.

Cross transect trends in the number and size of aspen and lodgepole (Table 2) demonstrate that lodgepole pine is infrequently encountered under aspen cover, but, where



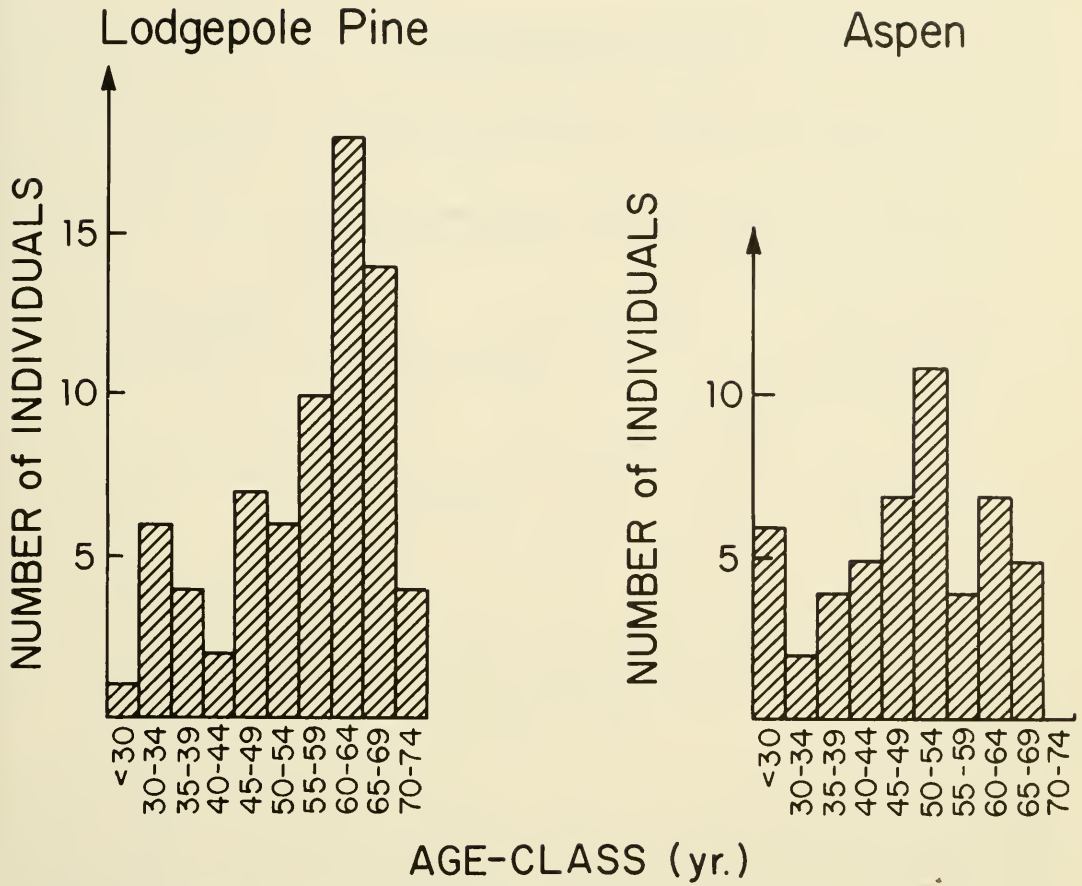


Fig. 2. Age-class distribution of lodgepole pine and aspen in cored transects. Histograms of the stem number by five-year age class intervals are shown for each species.

present, trees are generally large. Conversely, aspen is commonly encountered beneath lodgepole, although these trees are generally small. This pattern is more emphatically expressed in the understory; aspen saplings, seedlings, and standing dead stems (chiefly aborted suckers) are much more common under lodgepole cover than lodgepole is under aspen cover. The high number of aspen seedlings and standing dead stems under lodgepole cover is indicative of a successional strategy that relies on maintenance and gradual spread of the aspen root stock into the understory of adjacent conifer forests. The trend in mean tree diameter and in the number of both understory and dead stems across the transect clearly demonstrates the progressive spread of aspen across the ecotone (Table 2). The mean tree diameter of aspen and the total number of understory and dead

aspen stems steadily decline away from the aspen grove.

The collection of 72 lodgepole pine and 51 aspen tree cores was used to correlate age with stem diameter. Both species exhibited a comparable age-diameter relationship, the coefficient of variation of age (lodgepole = 0.22, aspen = 0.25) being less than the coefficient of variation of diameter (lodgepole = 0.38, aspen = 0.41) in each case. Furthermore, age was significantly correlated with diameter for each species (for aspen  $r = 0.654$ ,  $p < 0.001$ ; for lodgepole  $r = 0.665$ ,  $p < 0.001$ ). Lodgepole pine displayed a somewhat stronger tendency toward even-agedness than aspen, although both species exhibited unbroken representation in age ranges between 30 and 75 years. Fifty percent of the lodgepole stems were in the 60-to 75-year age range, suggesting colonization

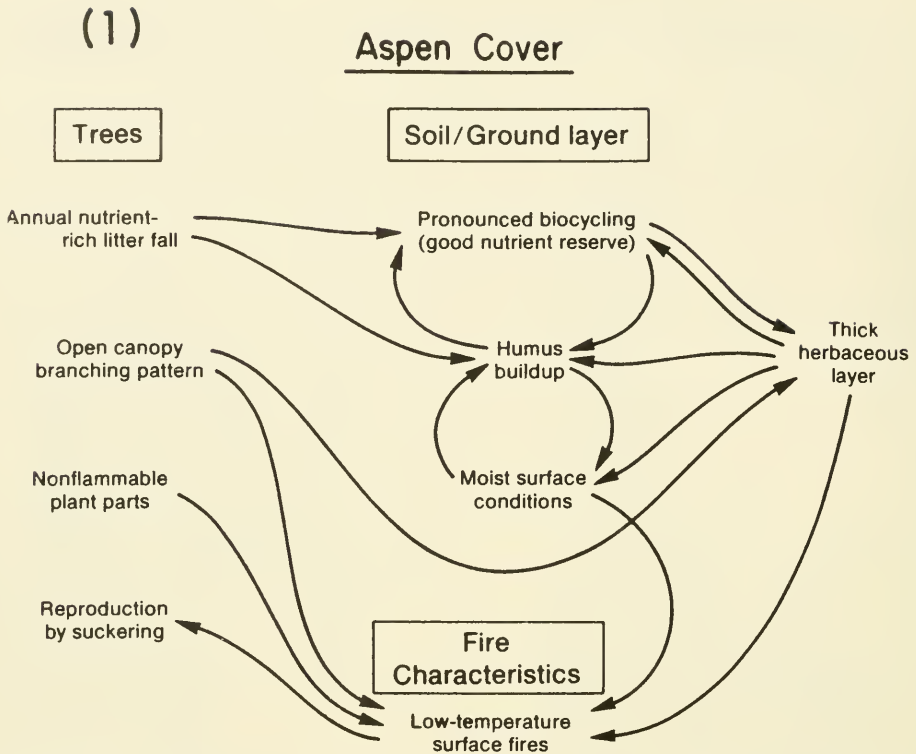


Fig. 3. Diagrammatic representation of the interactions among the dominant tree species, soil, ground layer vegetation, and fire characteristics under aspen and lodgepole pine forest cover.

immediately following the Bear Lake burn, and the maximum concentration of aspen stems (42 percent) occurred in the 45- to 60-year range (Fig. 1). The unsuppressed diameter growth rate of each species was determined using the 10 largest lodgepole and aspen trees cored. Our data reveal that following successful establishment unsuppressed lodgepole pine grows more rapidly than aspen ( $0.37 \text{ cm yr}^{-1}$  vs.  $0.32 \text{ cm yr}^{-1}$ ) on the study site. It should be cautioned that the period of establishment is generally several years longer for lodgepole pine produced from seed, which may require from 3 to 20 years to reach 0.2 m height (Romme and Knight 1981), than for aspen suckers, which may reach 3 m or greater height in 6 to 8 years (Jones and Trujillo 1975).

The composite diameter class diagram (Fig. 2), which is based on all seven belt transects and presented by cover type, does not show a tendency for concentration of lodgepole pine in larger size-classes even though many lodgepole trees are relatively

old, suggesting that older lodgepole stems may persist as suppressed individuals following postburn colonization for a lengthy period. Examination of these diameter-class diagrams reiterates that aspen is a fairly common understory tree beneath lodgepole forests, but only a few generally large-sized lodgepole individuals are scattered throughout the aspen canopy.

#### DISCUSSION

The soil profile and age structure differences between aspen and lodgepole pine stands suggest that each species, where dominant, reinforces a distinct group of vegetation-soil-fire interactions (Fig. 3). Furthermore, the persistence of these cover types appears to be more closely tied to stand history than to direct environmental gradients.

Under aspen cover, the deciduous, nutrient-rich foliage of aspen (Daubenmire 1953) and the dense herbaceous understory combine to enhance nutrient cycling and humifi-

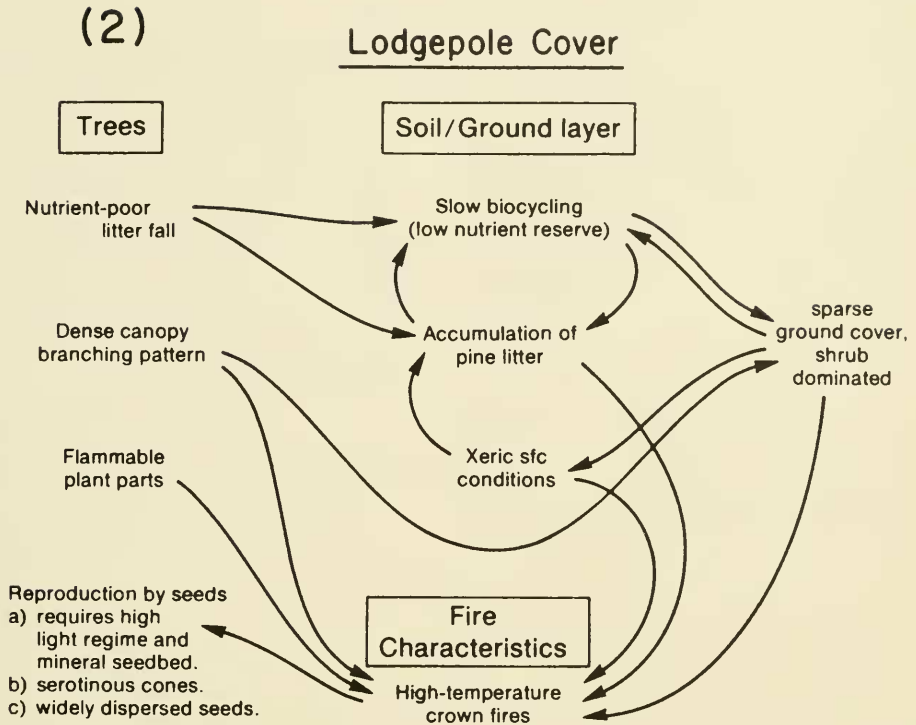


Fig. 3 continued.

cation, resulting in an increased cation exchange capacity and nutrient concentration in surface mineral horizons (Hoff 1957). The increased soil water retention conferred by the humus accumulation acts in concert with the ground cover (which buffers soil surface temperature and decreases windspeed, thus reducing evaporation) to increase the availability and effective use of soil moisture. Hence, aspen maintains a broad habitat range by direct enhancement of soil nutrient and moisture status (Lutz and Chandler 1946). On the contrary, the acidic lodgepole pine needles promote leaching, and the paucity of ground cover under lodgepole pine limits biocycling of nutrients; consequently, soils under lodgepole pine are often impoverished relative to adjacent aspen substrates (Hoff 1957). In addition, the mechanical resistance of pine needles to decomposition results in a decrease in humification and the buildup of pine needle litter.

Fire plays a prominent role in the perpetuation of discrete populations of both aspen and lodgepole pine (Fig. 3). Aspen dominance is maintained on a site through stimu-

lation of vegetative propagation following low-temperature surface fires, presumably through reduction of apical dominance (Daniel 1980). The buildup of surface fuels by the thick herbaceous layer, the mesicness of the ground layer, and the relative openness of the aspen canopy favor light-burning surface over crown fires (Horton and Hopkins 1965). Because of its suckering habit, aspen can sustain and is capable of slowly expanding local populations vegetatively into adjacent favorable sites. The ability of aspen to sucker in relatively dense shade facilitates this spread. Continued aspen dominance on a site requires the perpetuation of a surface fire regime that releases advance regeneration (Marks 1974, Oliver 1981) and stimulates vigorous reestablishment of aspen suckers. In the absence of fire, eventual ascendance of more tolerant conifer species often does not preclude the persistence of the aspen root stock in a suppressed condition (Marr 1961). Dependence on the maintenance of a "parental" aspen root stock is necessary to offset the competitive superiority of lodgepole pine (and other conifers) when both species are es-

tablished from seed, and favors persistent recolonization by aspen following light surface fires.

In lodgepole forests a denser canopy branching network, greater leaf area index, and a high resin production combine with a paucity of undergrowth to favor hot crown fires. By creating high surface light levels and mineralizing the litter layer, crown fires create a favorable seedbed for lodgepole pine establishment and trigger a wave of lodgepole pine regeneration that manifests itself in a tendency toward even-agedness in Rocky Mountain lodgepole forests. This contagious postburn colonization pattern is facilitated by lodgepole pine's lightweight, easily wind-dispersed seeds and rapid growth rate following seedling establishment on disturbed sites (allowing colonization from a remote seed source). Furthermore, colonization of severely burned sites by lodgepole pine is reinforced locally by partial core serotiny (Fowells 1965). In addition to favoring lodgepole establishment, severe burns inhibit aspen suckering, because most suckers develop from roots which are within 5 cm of the soil surface, and hence are easily killed in a hot fire (Daniel 1980).

The persistence of both aspen and lodgepole pine populations on sites with little evidence of successional alteration suggests that both species can be expected to maintain dominance for extended periods, in accordance with Egler's (1954) view of vegetation development. Only with prolonged fire exclusion are stands likely to be invaded and replaced by more tolerant conifers. Moreover, changes in dominance on a site appear to be related to the character of initiating disturbances (Henry and Swan 1974, Anderson and Holte 1981) and the differential reproductive habits of each species. A low-temperature surface fire regime favors the maintenance and gradual spread of aspen dominance by aggressive suckering. Stand-destroying crown fires open sites to rapid colonization by lodgepole pine, and repeated crown fires reinforce lodgepole pine dominance.

In summary, both trembling aspen and lodgepole pine are successful colonizer species in the southern Rocky Mountain region, although they accomplish colonization and

persistence in different ways. Aspen perpetuates itself through time on suboptimal sites by its suckering habit that rapidly recolonizes lightly burned sites, by promotion of a favorable surface fire regime, and by enhancement of site quality through improved soil water and nutrient retention capacity. Lodgepole pine, which develops more rapidly from seed than aspen and has easily dispersed seeds, is able to preempt aspen on optimal sites, and exhibits a relatively even-aged, contagious colonization pattern following stand-destroying crown fires.

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